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Research Article

# Two new species of *Entoloma* subgenus *Cyanula* (*E. alpigenum* and *E. muscicola*) from montane forests of Azad Jammu and Kashmir, Pakistan (Agaricales, Entolomataceae)

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## Abstract

Two new species of genus *Entoloma* in subgenus *Cyanula*, *Entoloma alpigenum* and *Entoloma muscicola* are described from the mixed forests of Azad Jammu and Kashmir, Pakistan. *Entoloma muscicola* is characterized by a cuspidate, deep brown pileus with wavy margins, distant pale yellow lamellae, weakly angled mono-gutulate basidiospores, predominantly two-spored basidia, and clavate cheilocystidia with wavy apical caps. In contrast, *Entoloma alpigenum* is characterized by a light brown, slightly squamulose pileus, pale yellowish lamellae, larger 5–7 angled mono-gutulate basidiospores and cylindrical to flexuose cheilocystidia. Both species are ecologically associated with high-altitude mixed forests. Phylogenetic analyses have placed these new species in subgenus *Cyanula*, forming sister clades within section *Griseocyanea*, which support their distinct taxonomic status. Illustrated descriptions of their macro- and microscopic features and phylogenetic analyses, based on nrITS, nrLSU, mtSSU and *rpb*2 regions are provided.

**Key words:** Entolomataceae, mixed and coniferous forests, multigene phylogeny, mushrooms, new species

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## Introduction

*Entoloma* (Fr.) P.Kumm. (Agaricales, Entolomataceae) is one of the largest and most morphologically diverse genera of agaricoid fungi. It currently comprises about 2,000 species distributed worldwide from tropical to temperate regions (Noordeloos et al. 2022a). These species are characterized by pinkish to reddish-brown spore prints, angular basidiospores with distinct facets, and typically adnate lamellae (Co-David et al. 2009). They exhibit remarkable morphological diversity, ranging from mycenoid and collybioid to tricholomatoid and omphalinoid forms, making taxonomic delimitation challenging (Co-David et al. 2009; Noordeloos and Gates 2012; Morgado et al. 2013; He et al. 2019).

Most species of *Entoloma* are terrestrial saprotrophs involved in litter decomposition, though some are biotrophic or ectomycorrhizal (Co-David et al. 2009; Morgado et al. 2013). Historically, *Cyanula* was introduced by Romagnesi (1974) as a section within *Rhodophyllus* Quél. (= *Entoloma*) based on morphological characters. The combination *Entoloma* sect. *Cyanula* (Romagn.) Noordel. was later included within *Entoloma* subg. *Leptonia sensu lato*. Traditionally, *Leptonia* was divided into three sections *Leptonia*, *Cyanula*, and *Griseorubida* (Noordeloos 2004) but subsequent molecular analyses revealed this grouping to be polyphyletic. Section *Leptonia* belongs to the *Nolanea–Claudopus* clade, while *Cyanula* and *Griseorubida* cluster within the *Inocephalus–Cyanula* clade (Co-David et al. 2009). Morphologically, species of sect. *Leptonia* exhibit clamp connections, whereas those of *Cyanula* lack them. Based on these distinctions, sect. *Cyanula* was elevated to subgenus rank (Noordeloos and Gates 2012; Noordeloos et al. 2022a).

Members of subg. *Cyanula* are typically recognized by their bluish to violaceous basidiomata, smooth basidiospores, absence of clamp connections, and ecological preference for woodland habitats. *Entoloma* species have been well studied in Europe and East Asia, their diversity in South Asia remains poorly documented. In Pakistan, only 14 taxa of *Entoloma* have been reported (Ahmad et al. 1997; Izhar 2022; Fatima et al. 2023; Khalid et al. 2024; Khan et al. 2026), and molecular data remain scarce. During a survey of mycobiota in Azad Jammu and Kashmir, Pakistan, two new species of *Entoloma* subgenus *Cyanula* were discovered. These new species are described based on morphology and multigene phylogenetic analyses based on four markers nrITS, nrLSU, mtSSU and *rpb*2.

## Material and methods

### Morphological and microscopic studies

Basidiomata were collected from coniferous mixed forests comprising *Pinus*, *Cedrus*, and *Abies* species in District Bagh, Azad Jammu and Kashmir, during the rainy seasons of 2019–2021. In situ, photographs of the basidiocarps were taken using Nikon D70S and D300S camera. Morphological characteristics were recorded from fresh specimens, and colors were designated using the mColorMeter application (Yanmei He, Mac App Store). Voucher specimens of the newly described species were deposited in the Herbarium of the Institute of Botany, University of the Punjab, Lahore, Pakistan.

Microscopic examination was performed on freehand sections of fresh and dried specimens mounted in 5% (w/v) aqueous potassium hydroxide (KOH) solution, using a Meiji Techno MX4300H compound microscope. A total of 30 basidiospores, basidia, cystidia, and hyphae from the pilei were measured from each collection. The notation “n/m/p” denotes the number of basidiospores measured from m fruit bodies of p collections. Basidiospore dimensions are presented as length × width (L × W), average length × average width (av. L × av. W), and average quotient (av. Q), with extreme values given in parentheses. The range represents at least 90% of the values. Measurements include the arithmetic mean of spore length and width. Additionally, scanning electron microphotographs were obtained at the University of Vienna, Austria.

## Molecular study

### Extraction, amplification and sequencing of DNA

Genomic DNA was extracted using either the DNeasy Plant Mini Kit (QIAgen GmbH, Hilden, Germany) or the Thermo Scientific GeneJET Plant Genomic DNA Purification Kit (Thermo Fisher Scientific Inc., Waltham, Mass., USA). Four regions were amplified and sequenced: ITS, LSU, mtSSU, and *rpb*2. The primer pairs used were ITS4/ITS5 (White et al. 1990) for ITS; LR0R/LR5 (Vilgalys and Hester 1990) for LSU; brpb2-6F/brpb2-7.1R or frpb2-7cR (Matheny 2005) for *rpb*2 and MS1 & MS2 (White et al. 1990) for mtSSU. PCR was performed in a 10 µL reaction volume consisting of 5 µL Biomed 2× Taq Plus PCR MasterMix (Biomed, Beijing, China), 3.9 µL $ddH_2O$, 0.3 µL of each primer (10 µmol/L), and 0.5 µL DNA template. PCR products were purified using an enzymatic PCR cleanup (Werle et al. 1994) as described by Voglmayr and Jaklitsch (2008). DNA was cycle-sequenced using the ABI PRISM Big Dye Terminator Cycle Sequencing Ready Reaction Kit v3.1 (Applied Biosystems, Warrington, UK). Sequencing was performed on an automated DNA sequencer (ABI 3730xl Genetic Analyzer, Applied Biosystems). Chromatograms were checked and assembled using SeqmanII v.5.07 (Dnastar Inc.).

### Phylogenetic analyses

A total of 149 sequences (42 ITS, 33 LSU, 15 *rpb*2, 17 mtSSU given in Table 1) were used to construct multigene phylogram based on Bayesian inference (BI) and Maximum likelihood (ML). The selection of sequences for the phylogenetic analyses were based on the results of ITS BLAST and from recent articles (Noordeloos et al. 2022b; Chen et al. 2025; Khan et al. 2026). Three species of *Entoloma* subg. *Nolanea* i.e *E. sericeum* and *E. atropapillatum* were designated as outgroups. Sequences for each locus were aligned separately using MAFFT (online server) with automatic algorithm selection (Katoh et al. 2019). First, phylogenetic trees were constructed separately for each region and their congruence were checked. Bayesian inference (BI) was conducted in MrBayes v.3.2.7a (Ronquist et al. 2012) with each partition (ITS, LSU, RPB2, mtSSU) assigned a GTR+I+G substitution model. Maximum likelihood (ML) analysis in IQ-TREE v.2.1.2 (Nguyen et al. 2015), was performed using the same GTR+I+G model for all partitions, with 1,000 ultrafast bootstrap replicates to assess node support.

## Results

### Molecular phylogenetic analyses (Fig. 1)

The combined dataset included 3780 nucleotide sites (ITS: 1–808 bp; LSU: 809–1910 bp; *rpb*2: 1911–3179 bp and mtSSU: 3179–3780 bp) including gaps. The bestfit evolutionary model selected for the concatenated analysis was TIM2+F+I+G4 model. The BI phylogenetic analysis was stopped after 5,400,000 generations, when the average standard deviation of split frequencies converged to 0.009874. For the maximum likelihood (ML)

**Table 1.** Sequences used for phylogenetic analyses in this study. Newly generated sequences are shown in and '–' indicating sequence unavailability.

| Species | Voucher/strain | Country | GenBank Accession Numbers | | | | Reference |
|---|---|---|---|---|---|---|---|
| | | | ITS | LSU | *rpb2* | mtSSU | |
| ***Entoloma alpigenum*** | **LAH38754** | **Pakistan** | **PX687957** | **PX687958** | **PX694301** | **PX693682** | **This study** |
| ***E. alpigenum*** | **WU48890** | **Pakistan** | **PX696031** | **PX687959** | **PX694300** | **–** | **This study** |
| ***E. alpigenum*** | **NALA-030** | **Pakistan** | **PX696032** | **PX687960** | **–** | **PX693683** | **This study** |
| *Entoloma ammophilum* | L0608224 | Netherlands | MW934591 | MZ333146 | – | – | Crous et al. (2021a) |
| *E. atropapillatum* | FK0898 | Brazil | KF679354 | KF738940 | MH190107 | KF738929 | Karstedt et al. (2020) |
| *E. brunneicoeruleum* | L0608198 | Brazil | MZ145166 | – | – | – | Dima et al. 2021 |
| *E. caespitosum* | GDGM24025 | China | JQ281490 | JQ410327 | OR916407 | OR912420 | He et al. (2012) |
| *E. caespitosum* | GDGM27564 | China | JQ281477 | JQ320130 | JQ993078 | JQ993070 | He et al. (2012) |
| *E. fuscosquamosum* | iNAT:30847414 | USA | MZ268031 | – | – | – | Unpublished in GenBank |
| *E. griseocyaneum* | LE254351 | Russia | KC898444 | KC898498 | – | KC898463 | Morozova et al. (2014) |
| *E. griseocaeruleum* | CME13 | Panama | MZ611624 | MZ611624 | – | – | Reschke et al. (2022a) |
| *E. holmvassdalenense* | O:F-304575 | Norway | MZ869018 | MZ678746 | – | – | Reschke et al. (2022a) |
| *E. incanum* | LE311794 | Russia | OK161249 | OK161276 | – | – | Crous et al. (2021b) |
| *E. incanum* | LE312503 | Sweden | OK161247 | OK161275 | – | – | Crous et al. (2021b) |
| *E. mastoideum* | D321 | Thailand | OR066303 | OR066336 | – | OR066375 | Pringsulaka et al. (2024) |
| *E. mastoideum* | D322 | Thailand | OR066304 | OR066337 | – | OR066376 | Pringsulaka et al. (2024) |
| *E. montanum* | GB:0191631 | Sweden | MW340897 | – | – | – | Noordeloos et al. (2021) |
| *E. montanum* | OF-252062 | Norway | MW340877 | – | – | – | Noordeloos et al. (2021) |
| ***E. muscicola*** | **LAH38755** | **Pakistan** | **PX687953** | **PX687956** | **PX693684** | **PX693681** | **This study** |
| ***E. muscicola*** | **WU48891** | **Pakistan** | **PX687954** | **PX687955** | **PX694299** | **PX693680** | **This study** |
| *E. nigroflavescens* | FA1726 | France | MZ198883 | – | – | – | Buyck et al. (2022) |
| *E. nigroflavescens* | FA4277 | France | MZ198884 | – | – | – | Buyck et al. (2022) |
| *E. orientosinense* | HFJAU2920 | China | PQ584688 | PQ584708 | PQ617187 | – | Chen et al. (2025) |
| *E. orientosinense* | HFJAU4048 | China | PQ584689 | PQ584709 | PQ617188 | – | Chen et al. (2025) |
| *E. praegracile* | GDGM29251 | China | JQ281482 | JQ320129 | JQ993077 | JQ993072 | He et al. (2013) |
| *E. serrulatum* | LE254361 | Russia | KC898447 | KC898501 | – | KC898466 | Morozova et al. (2014) |
| *E. sericeum* | KaiR1259 | Sweden | OL338182 | OL338182 | OL405219 | OL338493 | Reschke et al. (2022b) |
| *E. sericeum* | KaiR237 | Germany | OL338118 | OL338542 | OL405220 | OL338494 | Reschke et al. (2022b) |
| *E. subfarinaceum* | 127466550 | USA | OP470463 | – | – | – | Unpublished in GenBank |
| *E. subfarinaceum* | SAT1518702 | USA | KY777374 | – | – | – | Noordeloos et al. (2021) |
| *E. subpraegracile* | HFJAU3878 | China | PQ584693 | PQ584720 | PQ617199 | – | Chen et al. (2025) |
| *E. subpraegracile* | HFJAU5175 | China | PQ584703 | PQ584715 | PQ617192 | – | Chen et al. (2025) |
| *E. subpraegracile* | HFJAU5115 | China | PQ584699 | PQ584713 | PQ617194 | – | Chen et al. (2025) |
| *E. subpraegracile* | HFJAU5140 | China | PQ584702 | PQ584714 | PQ617195 | – | Chen et al. (2025) |
| *E. subtenuicystidiatum* | GDGM29246 | China | JQ320114 | JQ320132 | – | – | He et al. (2013) |
| *E. subtenuicystidiatum* | GDGM28459 | China | JQ320109 | JQ320116 | – | JQ99307 | He et al. (2013) |
| *E. turci* | FA4328 | France | OR419871 | – | – | – | Unpublished in GenBank |
| *E. turci* | F-2783 | Sweden | PQ652635 | PQ652635 | – | – | Unpublished in GenBank |
| *E. violaceoserrulatum* | JV8329F(TUR) | Finland | MF476913 | MF487803 | – | MF476923 | Morozova et al. (2018) |
| *E. wuyishanense* | HFJAU3871 | China | PQ584692 | PQ584717 | PQ617197 | – | Chen et al. (2025) |
| *E. wuyishanense* | HFJAU3874 | China | PQ584694 | PQ584718 | PQ617198 | – | Chen et al. (2025) |
| *E. yanacolor* | QCAM6312 | Ecuador | MG947210 | MG947210 | – | – | Crous et al. (2018) |

analysis, models were selected using the Bayesian Information Criterion (BIC), yielded a final log-likelihood value of -18410.138.

The phylogenetic tree is shown in Fig. 1. The two new species clustered within the subgenus *Cyanula* clade, forming a distinct and well-supported clade (100% BS/1.00 PP) as sister species.

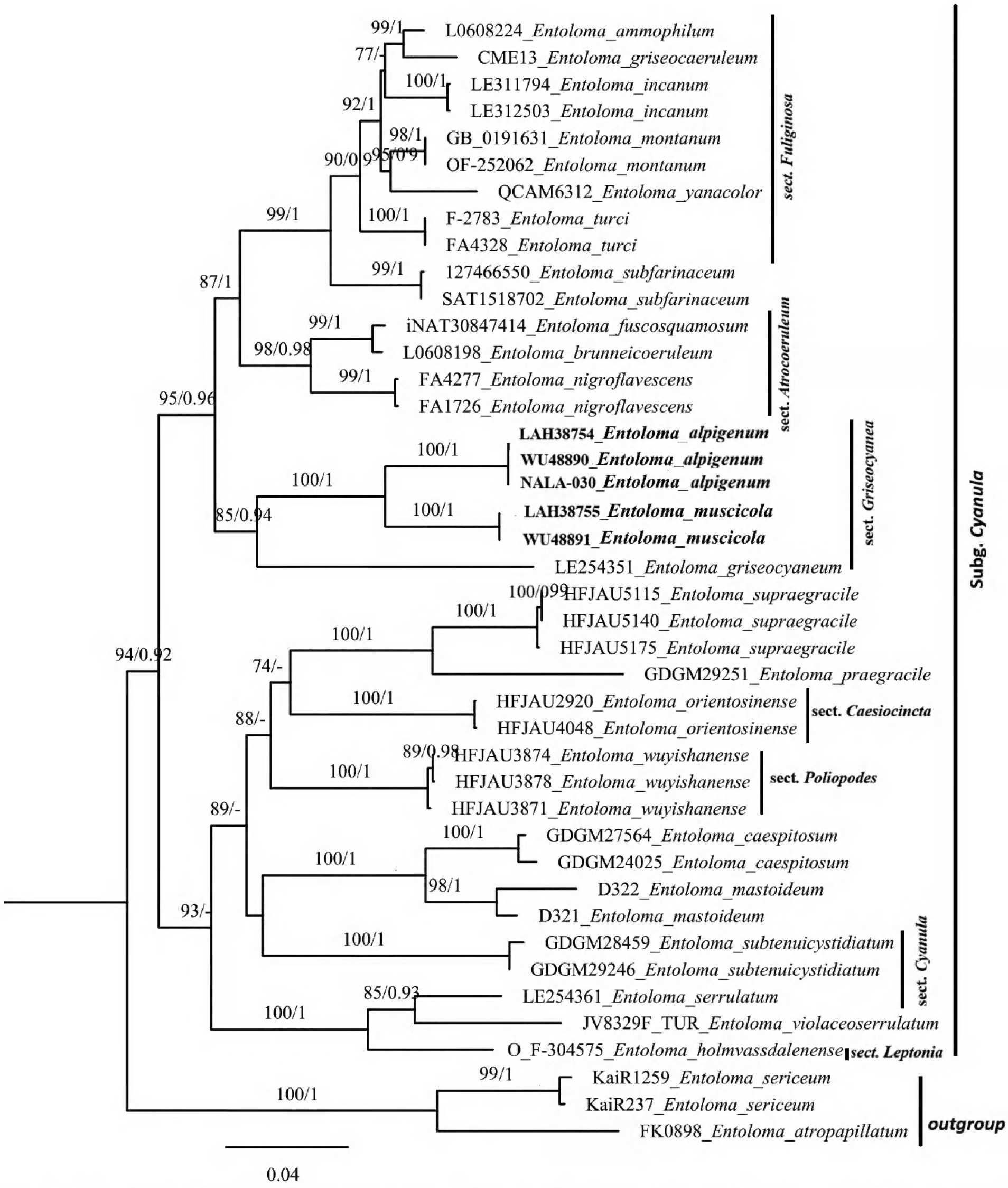


**Figure 1.** Phylogram of *Entoloma* subg. *Cyanula* spp. generated by Bayesian inference (BI) analysis based on dataset of nrITS, nrLSU mtSSU and *rpb2* sequences. The tree is rooted with *E. sericeum* and *E. atropapillatum*. Bayesian inference (BI-PP) ≥ 0.90 and ML bootstrap proportions (ML-BP) ≥ 70% are indicated as PP/BP. The new taxa are marked in bold.

## Taxonomy

***Entoloma alpigenum* Khurshid & Naseer, sp. nov.**
MycoBank No: 861488
Figs 2–4

**Etymology.** The specific epithet "*alpigenum*" is derived from "originating from alpine regions," reflecting the species' high-elevation distribution.

**Holotype.** Pakistan • Azad Jammu and Kashmir, Bagh District, Choki City, 33.98°N, 73.78°E, alt. 2,625 m, 20 September 2020, collected by Rubab Khurshid, LAH38754.

**Diagnosis.** *Entoloma alpigenum* is characterized by its light brown, slightly squamulose pileus, whitish–cream context, lacking gray-blue pigments, cylindrical to flexuose cheilocystidia and heterodiametric, 5–7-angled basidiospores. In contrast, its closely related species *E. griseocyaneum* shows bluish tones and slightly different cheilocystidia. Its high-elevation alpine habitat (2,625 m) together with macroscopic and microscopic features clearly distinguish it from its close relatives.

**Macromorphology.** Basidiomata medium-sized. Pileus 1.5–9.5 cm across, convex to plano-convex, becoming slightly depressed at the center with age. Surface dry, rugulose to finely squamulose at the disc, smoother toward the margin. Centre light brown (5YR 6/4), progressively becoming pale brown to cream (5Y 9/4) toward the margin. Margin entire to slightly striate, sometimes cracked in mature basidiomata. Context whitish to cream (5Y 9/2), unchanging when cut. Lamellae free, close, with entire to slightly serrulate edges, whitish to cream (10Y 9/2), becoming pale yellowish (10Y 9/4) in maturity. Lamellulae arranged in three to four tiers, irregular in length and distribution. Stipe 4.8–6.5 × 0.3–0.6 cm, cylindric, concolorous with the pileus surface; base whitish (5Y 9/2), becoming pale yellowish (5Y 9/4) toward the apex. Surface smooth; stipe stuffed; base subbulbous to slightly swollen, often attached to a whitish rhizomorphic mass. Annulus and volva absent. Smell and taste not recorded.

**Micromorphology.** Basidiospores [60/3/2], (7.9–)9.1–10.8(–11.3) × (6.0–)6.2–8.8(–9.1) µm, av. L × av. W = 10.1 × 6.9 µm, Q = 1.1–1.6 µm, avQ = 1.39, heterodiametric, 5–7 angled in side view, with weak angles, smooth, thin-walled, epiculus present, non-granulate, mono gutulate, hyaline in 5% KOH. Basidia (38.3–)39.4–42.5(–49.2) × (7.1–)7.3–10.3(–11.2) µm, av. L × av. W = 40.6 × 8.9 µm, clavate, mostly 4-spored, occasionally 2-spored, with pointed sterigmata, non-guttulate, non-granulate, sessile at the base, and without clamp connections, hyaline in 5% KOH. Cheilocystidia (29.6–)31.2–36.7(–44.8) × (3.9–)4.1–5.4(–5.8) µm, av. L × av. W = 34.2 × 5.3 µm, cylindrical to flexuous, thin-walled, composed of 2–3 basal cells, without clamp connection, and hyaline in 5% KOH; pleurocystidia absent. Stipitipellis composed of septate, unbranched, thin-walled hyphae (10.1–)12.5–15.8(–17.4) µm in diameter, lacking clamp connections, with caulocystidia not observed. Pileipellis a cutis of crowded, filamentous, septate hyphae (2.8–)4.7–10.1(–11.4) µm in diameter, rarely branched, with well-differentiated terminal cells, clamp connections present, pileocystidia absent, non-guttulate, thin-walled, and hyaline in 5% KOH.

**Habitat.** Solitary or scattered on soil or moss under coniferous forest.

**Distribution.** Currently only known from Azad Jammu and Kashmir, Pakistan.

**Figure 2.** Morphology of *Entoloma alpigenum* (**A–D**) LAH38754, holotype. **A.** Lamellae and stipe view; **B, C.** Pileus view; **D.** Lamellae and stipe view. Scale bars: 1.7 cm (**A**); 1.5 cm (**B**); 4.1 cm (**C**); 3.3 cm (**D**).

**Additional specimen examined.** Pakistan • Azad Jammu and Kashmir, Bagh District, Ochar City, 33.98°N, 73.78°E, alt. 1,611 m, 24 August 2021, collected by Rubab Khurshid, WU48890; Pakistan • Azad Jammu and Kashmir, Bagh District, Ochar City, 33.98°N, 73.78°E, alt. 1,454 m, 28 August 2021, collected by Rubab Khurshid, Nala-030.

**Notes.** *Entoloma alpigenum* belongs to the subgenus *Cyanula* and is most closely related to the European species *E. griseocyaneum*, but differs in macroscopic coloration, spore dimensions, and cystidial morphology. It is also comparable to Asian species such as *E. nigroflavescens* and *E. fuscosquamosum*. *Entoloma alpigenum* differs from *E. griseocyaneum* in its light brown, slightly squamulose pileus and pale yellowish lamellae, entirely lacking bluish pigmentation, whereas *E. griseocyaneum* is characterized by a grayish-blue to bluish-black pileus with bluish lamellae when young. In addition, *E. alpigenum* possesses smaller basidiospores (9.1–10.8), while *E. griseocyaneum* has

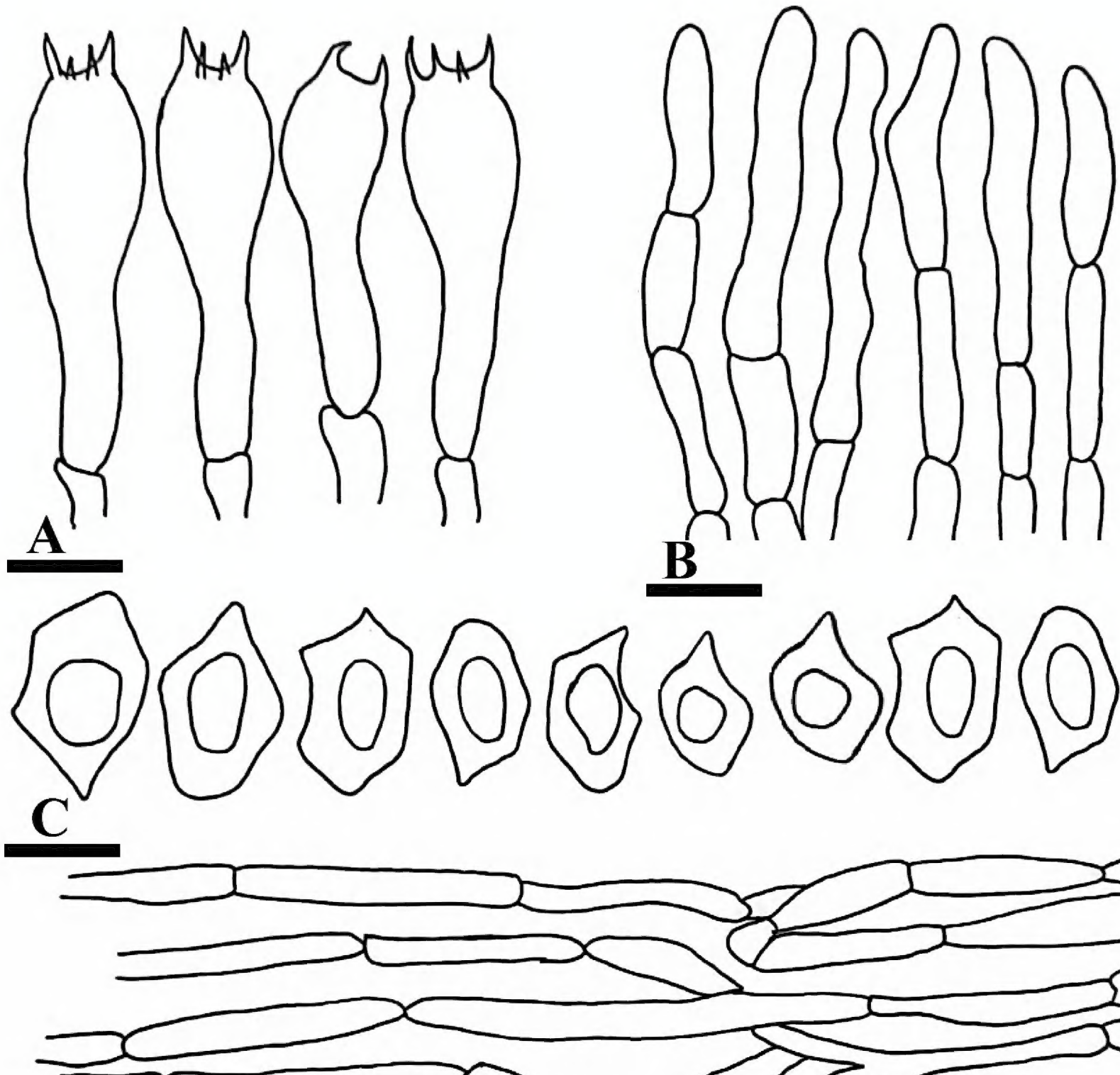


**Figure 3.** Anatomy of *Entoloma alpigenum* (**A–E**). **A.** Basidia; **B.** Cheilocystidia; **C.** Basidiospores; **D.** Piliepellis; **E.** Stipitipillis. Scale bars: 1.3 µm (**A**); 3 µm (**B**); 8 µm (**C**); 14 µm (**D**); 10 µm (**E**).

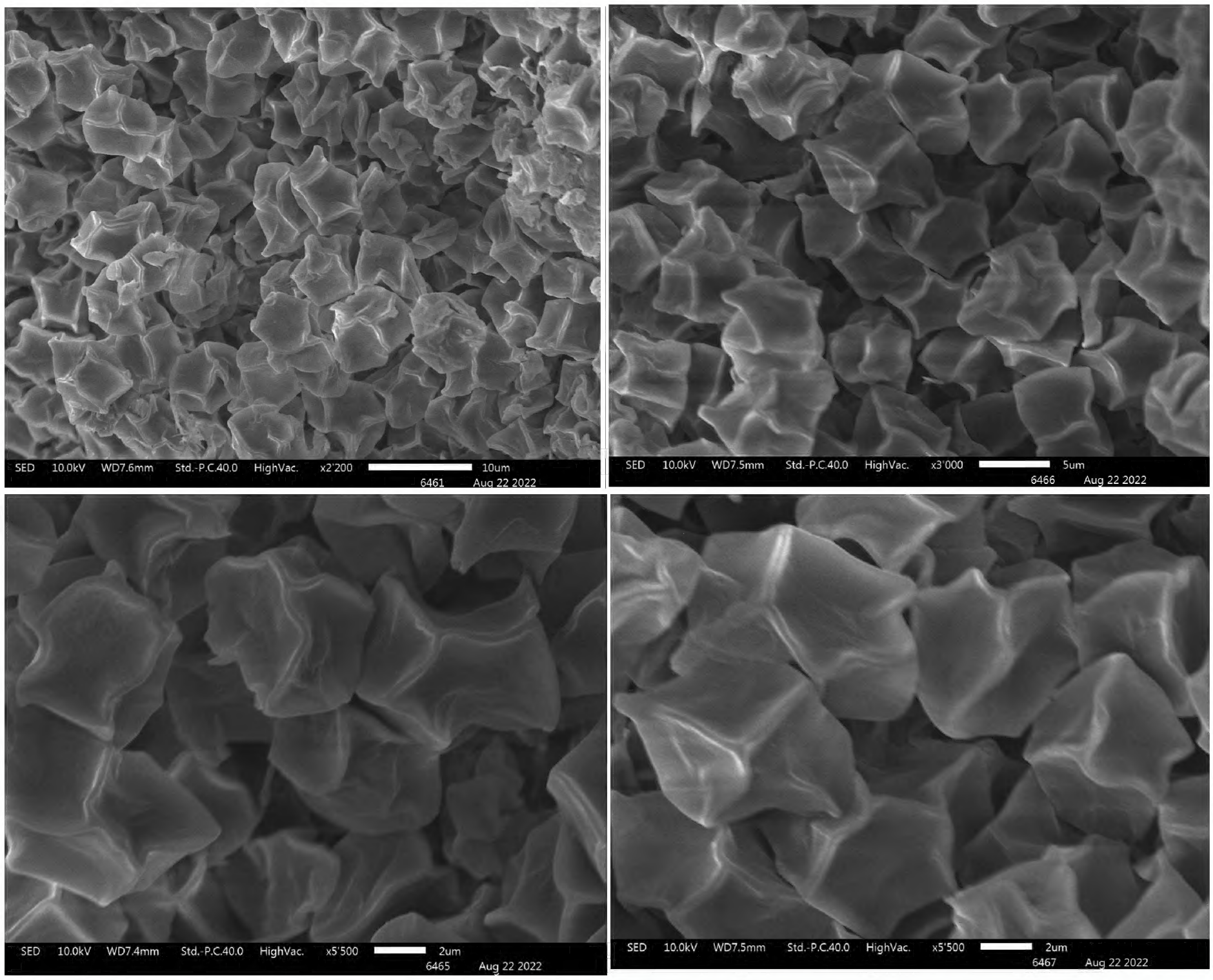
SED 10.0kV WD7.6mm Std.-P.C.40.0 HighVac. x2'200 10um 6461 Aug 22 2022
SED 10.0kV WD7.5mm Std.-P.C.40.0 HighVac. x3'000 5um 6466 Aug 22 2022
SED 10.0kV WD7.4mm Std.-P.C.40.0 HighVac. x5'500 2um 6465 Aug 22 2022
SED 10.0kV WD7.5mm Std.-P.C.40.0 HighVac. x5'500 2um 6467 Aug 22 2022

**Figure 4.** Scanning Electron Microscopy of *Entoloma alpigenum*.

comparatively larger spores (9–13.5) (Noordeloos 1992; Brandrud et al. 2012). Similarly, the pileus of *E. alpigenum* is paler and less distinctly fibrillose than the dark brown to blackish-brown, more strongly squamulose pileus of *E. nigroflavescens* and *E. fuscosquamosum* (Noordeloos 1992; Largent 1994a).

Phylogenetically, *Entoloma alpigenum* belong to the subgenus *Cyanula* as a distinct, well-supported lineage, forming a close relationship with *E. griseocyaneum*. Despite the close phylogenetic affinity, both species remain clearly separable by their morphological characters. Microscopically, *E. alpigenum* has larger basidiospores (9.1–10.8 × 6.2–8.8 µm) with 5–7 weak angles, which contrasts with the smaller, more sharply angular spores commonly found in *E. griseocyaneum* (Noordeloos 1992; Kokkonen 2015). The cylindrical to flexuose cheilocystidia of *E. alpigenum* (av. 39.6 × 5.3 µm) are also distinctive. In *E. griseocyaneum*, cheilocystidia when present are typically clavate to lageniform, not narrow and flexuose. In *E. fuscosquamosum*, cystidia are broader and fusiform, while *E. nigroflavescens* lacks cheilocystidia entirely (Noordeloos 1988; Noordeloos 1992; Buyck et al. 2022). The absence of pleurocystidia and predominantly four-spored basidia are shared with some related species, but the overall combination of characters is unique. *E. alpigenum* inhabits high-altitude coniferous forests (1,611–2,625 m a.s.l.) of the western Himalayas. In contrast, *E. griseocyaneum* is distributed mainly in temperate European moss-rich

grasslands and woodland margins (Brandrud et al. 2012). Both *E. fuscosquamosum* and *E. nigroflavescens* generally occur at lower elevations and in more temperate forested habitats (Noordeloos 1992). *E. alpigenum* is strongly supported by three collections, confirming its distinct species identity.

***Entoloma muscicola*** **Khurshid & Naseer, sp. nov.**

MycoBank No: 861489

Figs 5–7

**Etymology.** The specific epithet "*muscicola*" refers to the moss-dwelling habit of the species.

**Holotype.** PAKISTAN • Azad Jammu and Kashmir, Bagh District, Choki City, 33.98°N, 73.78°E, alt. 1,811 m, 24 August 2020, collected by Rubab Khurshid (LAH38755).

**Diagnosis.** *Entoloma muscicola* is characterized by cuspidate pileus, distant lamellae, weakly angled mono-gutulate spores, distinctive clavate cheilocystidia and the absence of cellular pigments and clamp connections in the hyphae distinguishing it from closely related species including *E. griseocyaneum*, *E. fuscosquamosum*, and *E. nigroflavescens*.

**Macromorphology.** Basidiomata small to medium-sized. Pileus 1.0–5.7 cm across, ovoid to conical when young, becoming campanulate to cuspidate at maturity, with a distinctly darker deep brown umbonate center (2.5YR 1/8) gradually fading to light brown toward the margin (7.5YR 5/4). Surface dry, smooth to subtly shiny, striate to plicate toward the margin; margin wavy, striate, sometimes slightly uplifted. Context whitish to cream (5Y 9/2), unchanged when cut. Lamellae free, distant, with entire and even edges, whitish (10Y 9/2) to pale yellow (10Y 9/4). Lamellulae present, arranged in 3–4 tiers, regularly distributed. Stipe 3–7.4 × 0.2–0.5 cm, cylindrical, whitish (5Y 9/2) at the base becoming pale yellowish (5Y 9/4) toward the apex, surface smooth, hollow, subbulbous to slightly swollen at the base, often attached to a mass of whitish rhizomorphs. Annulus absent. Volva absent. Odor and taste not recorded.

**Micromorphology.** Basidiospores [60/3/2], (9.3–)9.7–11.6(–12.5) × (6.1–)6.3–7.9(–8.2) µm, av. L × av. W = 10.8 × 6.9 µm, Q = 1.2(–1.34)–1.7, avQ = 1.6, heterodiametric, 4–6 angled in side view, with weak angles; smooth, thin-walled; epiculus present; non-granulate; mono-guttulate; hyaline in 5% KOH. Basidia (34.4–)36.4–43.8(–46.0) × (8.8–)9.4–10.1(–10.4) µm, av. L × av. W = 39.3 × 10.0 µm clavate, tapering sharply toward the base; usually two sterigmata, rarely four; pointed ends; non-guttulate, non-granulated; base sessile; clamp connection absent; hyaline in 5% KOH. Cheilocystidia (30–)34.1–39.8(–45) × (7.8–)8.6–9.4(–10.5) µm, av. L × av. W = 36.8 × 9.1 µm, clavate, apex covered with wavy cap structure, thin walled, 1 celled base, hyaline in 5% KOH. Stipitipellis a cutis, hyphae (5.1–)5.6–6.8(–12.3) µm in diameter, septate, unbranched, thin walled, clamp connections absent, caulocystidia not observed, hyaline in 5% KOH. Pileipellis a cutis, hyphae (8.6–)8.8–12.5(–14.2) µm in diameter, septate, filamentous, crowded, un-branched, with well differentiated terminal cells, clamp connection absent, pileocystidia absent, non-guttulate, thin walled, hyaline in 5% KOH.

**Figure 5.** Morphology of *Entoloma muscicola* (**A–G**) LAH38755, holotype. **A.** Lamellae and stipe view; **B–D.** Pileus and stipe view; **E.** Lamellae and stipe view; **F.** Pileus and stipe view; **G.** Lamellae and stipe view. Scale bars: 1 cm (**A**); 3.5 cm (**B**); 2.5 cm (**C**); 2 cm (**D–F**).

**Habitat.** Found solitary or gregarious, dwelling on soil or moss under conifers.

**Distribution.** Currently only known from Azad Jammu and Kashmir, Pakistan

**Additional material examined.** Pakistan • Azad Jammu and Kashmir, Bagh District, Choki City, 33.98°N, 73.78°E, alt. 1,521 m, 28 August 2021, Collected by Rubab Khurshid, WU48891.

**Notes.** *Entoloma muscicola* is closely related to *E. griseocyaneum*, *E. nigroflavescens*, and *E. fuscosquamosum* but can be readily distinguished by a combination of morphological and ecological traits. Compared with

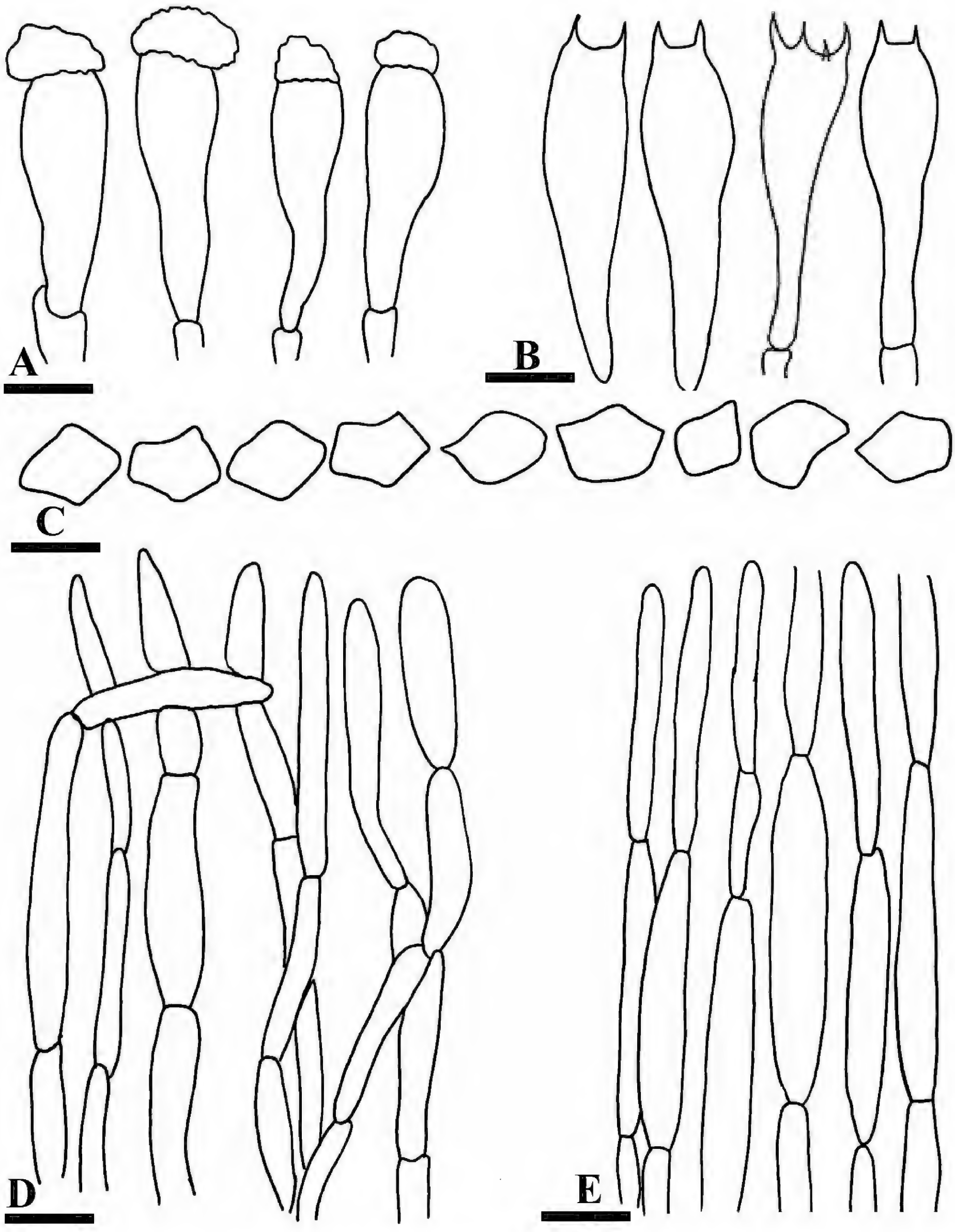


**Figure 6.** Anatomy of *Entoloma muscicola* (**A–E**). **A.** Cheilocystidia; **B.** Basidia; **C.** Basidiospores; **D.** Pileipellis; **E.** Stipitipellis. Scale bars: 8 µm (**A**); 10 µm (**B**); 7 µm (**C**); 12 µm (**D**); 10 µm (**E**).

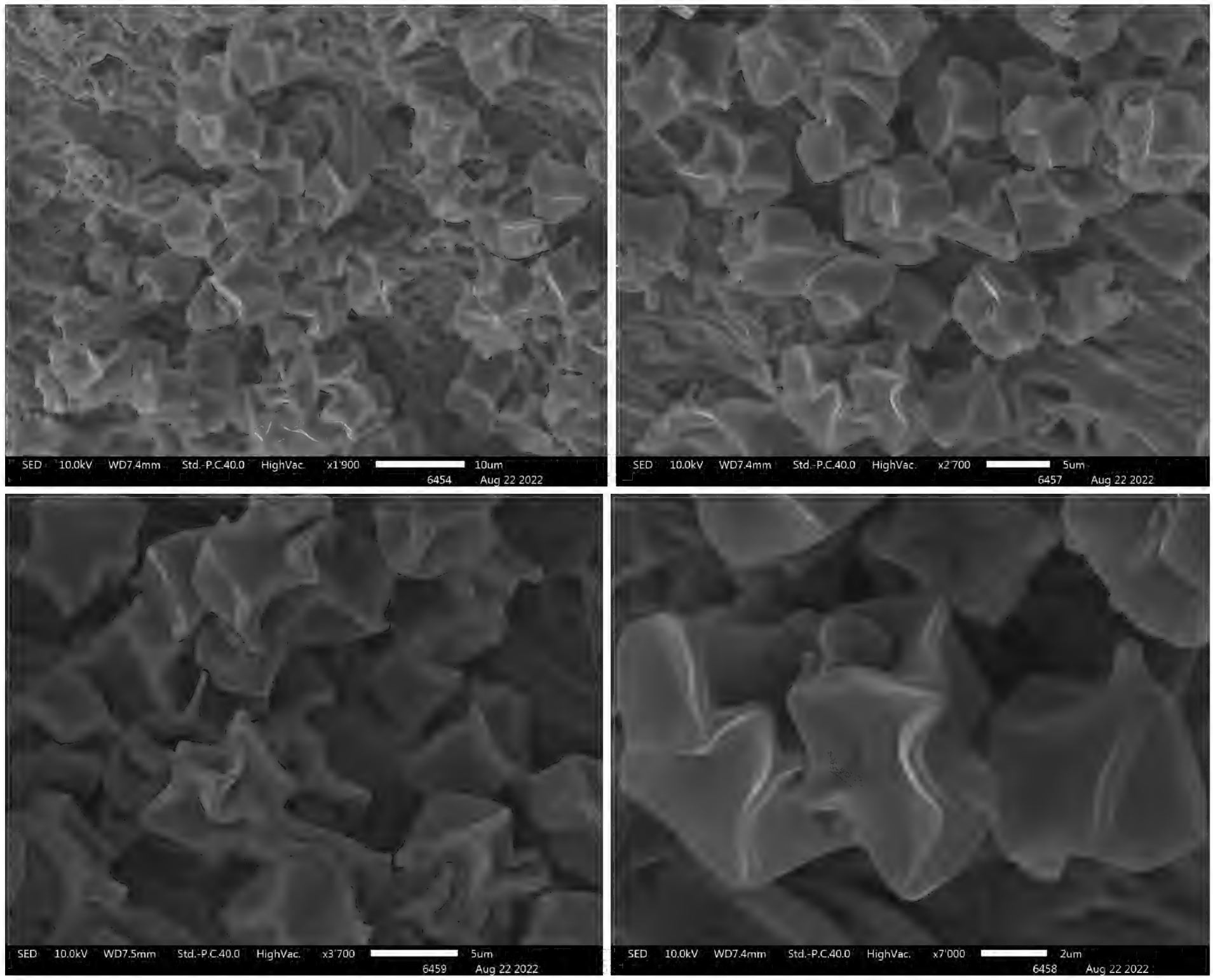
SED 10.0kV WD7.4mm Std.-P.C.40.0 HighVac. x1'900 10um
6454 Aug 22 2022
SED 10.0kV WD7.4mm Std.-P.C.40.0 HighVac. x2'700 5um
6457 Aug 22 2022
SED 10.0kV WD7.5mm Std.-P.C.40.0 HighVac. x3'700 5um
6459 Aug 22 2022
SED 10.0kV WD7.4mm Std.-P.C.40.0 HighVac. x7'000 2um
6458 Aug 22 2022

**Figure 7.** Scanning Electron Microscopy of *Entoloma muscicola*.

*E. griseocyaneum*, *E. muscicola* is readily distinguished by lacking gray-blue pigmentation in all parts of the basidiome and by having a brown to deep brown, cuspidate pileus with whitish to pale yellow lamellae. In contrast, *E. griseocyaneum* is characterized by bluish to gray-blue tones on the pileus and stipe and by producing distinctly more slender basidiomes (Fries 1821; Noordeloos 1992). *Entoloma muscicola* has clavate cheilocystidia with a wavy apical cap, and weakly 4–6-angled mono-gutulate basidiospores (av. 10.8 × 6.9 µm). *E. griseocyaneum* lacks cheilocystidia on the lamellar edge and produces 6-angled basidiospores (Noordeloos 1992; Buyck et al. 2022). Basidia in *E. muscicola* are predominantly 2-spored, rarely 4-spored, whereas related taxa *E. fuscosquamosum* and *E. griseocyaneum* typically have 4-spored basidia (Noordeloos 1992; Largent 1994a). Cheilocystidia in *E. muscicola* (36.8 × 9.1 µm) distinguish it from *E. nigroflavescens*, which lacks cheilocystidia, and from *E. fuscosquamosum*, which possesses broader, fusiform cheilocystidia (Noordeloos 1992; Buyck et al. 2022). The pileipellis forms a cutis of crowded filamentous hyphae with well-differentiated terminal cells, and clamp connections are absent. *Entoloma muscicola* occurs on soil or moss under montane mixed forests (*Pinus wallichiana* and *Cedrus deodara*) at ~1,811 m a.s.l., whereas *E. griseocyaneum* is typically associated with grasslands or subalpine pastures at lower to mid-elevations (Buyck et al.

2022) and *E. fuscosquamosum* occurs in temperate forests (Largent 1994b). Based on these differences and phylogeny, we introduce *E. muscicola* in section *Griseocyanea*; subgenus *Cyanula*, as a distinct species.

## Discussion

The present study significantly expands the documented diversity of *Entoloma* subgenus *Cyanula* in Pakistan and underscores the systematic complexity of this lineage in montane ecosystems. The recognition of *E. muscicola* and *E. alpigenum* introduces two previously undocumented phylogenetic lineages, indicating that *Cyanula* remains insufficiently explored in South Asia despite its global taxonomic importance within the genus. Both species are robustly assigned to *Cyanula* based on concordant evidence from diagnostic morphological characters and multilocus phylogenetic analyses. Phylogenetic reconstruction resolves *E. muscicola* and *E. alpigenum* as strongly supported sister taxa that are clearly distinct from morphologically similar species such as *E. nigroflavescens* and *E. fuscosquamosum*, supporting their interpretation as independent evolutionary lineages rather than geographic variants of previously described taxa. The close correspondence between micromorphological traits, particularly basidiospore morphology and cheilocystidial structure and molecular divergence, further substantiates their recognition as discrete species and contributes to refining species boundaries within *Entoloma*.

The occurrence of both taxa in high-altitude mixed forests suggests that elevational gradients may play an important role in diversification processes within *Entoloma*. *Entoloma alpigenum*, recorded at 2,625 m a.s.l., inhabits cooler, more humid, and comparatively undisturbed environments than many related lowland species. Such ecological conditions may facilitate isolation, limit gene flow, and promote adaptive differentiation, thereby fostering speciation in montane lineages of *Cyanula*. Although broader sampling is needed to rigorously test this hypothesis, the present findings indicate that high-elevation habitats in Pakistan likely represent significant reservoirs of undescribed fungal diversity.

Overall, this study highlights the value of integrative taxonomic approaches for revealing cryptic diversity in *Entoloma* and identifies high-altitude ecosystems in Pakistan as important yet underexplored centers of fungal biodiversity. Beyond its systematic implications, documenting diversity within *Entoloma* also holds applied relevance, as species of the genus are known to produce bioactive metabolites with potential agricultural, medicinal, and industrial applications.

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## Additional information

### Conflict of interest

The authors have declared that no competing interests exist.

## Ethical statement

No ethical statement was reported.

## Use of AI

No use of AI was reported.

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## Author contributions

Conceptualization: QL & AN. Data curation: RK & ANK. Formal analysis: RK & ANK. Investigation: AN & QL. Methodology: RK & AR. Resources: RK & QL. Software: RK & AN.

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## Data availability

All of the data that support the findings of this study are available in the main text.

## References

Ahmad S, Iqbal SH, Khalid AN (1997) Fungi of Pakistan. Sultan Ahmad Mycological Society of Pakistan, Department of Botany, University of the Punjab, Lahore.

Brandrud TE, Bendiksen E, Jordal JB, Skifte O (2012) *Entoloma* s.l. Fungi of Northern Europe 5: 1–480.

Buyck B, Eyssartier G, Armada F, Corrales A, Hembrom ME, Rossi W, Bellanger JM, Das K, Dima B, Ghosh A, Noordeloos ME, Parihar A, Krisai-Greilhuber I, Leonardi M, Manz C, Vera M, Vila J, Adamčíková K, Bizio E, Caboň M, Hampe F, Piepenbring M, Adamčík S (2022) Fungal biodiversity profiles 111–120. Cryptogamie. Mycologie 43(2): 23–61. https://doi.org/10.5252/cryptogamie-mycologie2022v43a2

Chen LG, Chen H, Ding L, Xu YQ, Zeng H, Wang SN, Yan JQ (2025) Four new species of *Entoloma* subgenus *Cyanula* (Entolomataceae, Agaricales) from subtropical regions of China. MycoKeys 116: 303. https://doi.org/10.3897/mycokeys.116.145568

Co-David D, Langeveld D, Noordeloos ME (2009) Molecular phylogeny and spore evolution of Entolomataceae. Persoonia-Molecular Phylogeny and Evolution of Fungi 23: 147–176. https://doi.org/10.3767/003158509X480944

Crous PW, Wingfield MJ, Burgess TI, Hardy GEStJ, Gené J, Guarro J, Baseia IG, García D, Gusmão LFP, Souza-Motta CM, Thangavel R, Adamčík S, Barili A, Barnes CW, Bezerra JDP, Bordallo JJ, Cano-Lira JF, de Oliveira RJV, Ercole E, Hubka V, Iturrieta-González I, Kubátová A, Martín MP, Moreau PA, Morte A, Ordoñez ME, Rodríguez A, Stchigel AM, Vizzini A, Abdollahzadeh J, Abreu VP, Adamčíková K, Albuquerque GMR, Alexandrova AV, Álvarez Duarte E, Armstrong-Cho C, Banniza S, Barbosa RN, Bellanger J-M, Bezerra JL, Cabral TS, Caboň M, Caicedo E, Cantillo T, Carnegie AJ, Carmo LT, Castañeda-Ruiz RF, Clement CR, Čmoková A, Conceição LB, Cruz RHSF, Damm U, da Silva BDB, da Silva GA, da Silva RMF, de Santiago ALCM, de Oliveira LF, de Souza CAF, Déniel F, Dima B, Dong G, Edwards J, Félix CR, Fournier J, Gibertoni TB, Hosaka K,

Iturriaga T, Jadan M, Jany J-L, Jurjević Ž, Kolařík M, Kušan I, Landell MF, Leite Cordeiro TR, Lima DX, Loizides M, Luo S, Machado AR, Madrid H, Magalhães OMC, Marinho P, Matočec N, Mešić A, Miller AN, Morozova OV, Neves RP, Nonaka K, Nováková A, Oberlies NH, Oliveira-Filho JRC, Oliveira TGL, Papp V, Pereira OL, Perrone G, Peterson SW, Pham THG, Raja HA, Raudabaugh DB, Řehulka J, Rodríguez-Andrade E, Saba M, Schauflerová A, Shivas RG, Simonini G, Siqueira JPZ, Sousa JO, Stajsic V, Svetasheva T, Tan YP, Tkalčec Z, Ullah S, Valente P, Valenzuela-Lopez N, Abrinbana M, Viana Marques DA, Wong PTW, Xavier de Lima V, Groenewald JZ (2018) Fungal planet description sheets: 716–784. Persoonia 40: 240–393. https://doi.org/10.3767/persoonia.2018.40.10

Crous PW, Cowan DA, Maggs-Kölling G, Yilmaz N, Thangavel R, Wingfield MJ, Noordeloos ME, Dima B, Brandrud TE, Jansen GM, Morozova OV, Vila J, Shivas R, Tan YP, Bishop-Hurley SL, Lacey E, Marney TS, Larsson E, Floch GL, Lombard L, Nodet P, Hubka V, Alvarado P, Berraf-Tebbal A, Reyes JD, Delgado G, Eichmeier A, Jordal JB, Kachalkin A, Kubátová A, Macia-Vicente JG, Malysheva E, Papp V, Rajeshkumar KC, Sharma A, Spetik M, Strašiftáková D, Tomashevskaya MA, Abad JA, Abad ZG, Alexandrova AV, Anand G, Arenas F, Ashtekar ND, Balashov S, Bañares Á, Baroncelli R, Bera I, Biketova AY, Blomquist CL, Boekhout T, Boertmann D, Bulyonkova T, Burgess TI, Carnegie A, Díaz JFC, Corriol G, Cunnington J, Cruz M, Damm U, Davoodian N, Santiago A, Dearnaley JDW, Freitas LWSd, Dhileepan K, Dimitrov RA, Piazza SD, Fatima S, Fuljer F, Galera H, Ghosh A, Giraldo A, Glushakova AM, Gorczak M, Gouliamova D, Gramaje D, Groenewald M, Gunsch CK, Gutiérrez A, Holdom D, Houbraken J, Ismailov A, Istel Ł, Iturriaga T, Jeppson M, Jurjević Ž, Kalinina L, Kapitonov VI, Kautmanová I, Khalid AN, Kiran M, Kiss L, Kovács Á, Kurose D, Kušan I, Lad S, Læssøe T, Lee HB, Luangsa-Ard JJ, Lynch M, Popov E, Matočec N, Reschke K (2021a) Fungal Planet description sheets: 1182–1283. Persoonia-Molecular Phylogeny and Evolution of Fungi 46: 313–528. https://doi.org/10.3767/persoonia.2021.46.11

Crous PW, Osieck ER, Jurjević Ž, Boers J, Iperen AV, Starink M, Dima B, Balashov S, Bulgakov T, Johnston PR, Morozova OV, Pinruan U, Sommai S, Alvarado P, Decock C, Lebel T, McMullan-Fisher SJM, Moreno G, Shivas R, Zhao L, Abdollahzadeh J, Abrinbana M, Ageev D, Akhmetova C, Alexandrova A, Altés A, Amaral AGG, Angelini C, Antonín V, Arenas F, Asselman P, Badali F, Baghela A, Bañares Á, Barreto RW, Baseia I, Bellanger J-M, Berraf-Tebbal A, Biketova AY, Bukharova N, Burgess TI, Cabero J, Camara MPS, Cano J, Ceryngier P, Chavez R, Cowan DA, Lima AFd, Oliveira R, denman S, Quynh DN, Dovana F, Duarte IG, Eichmeier A, Erhard A, Esteve-Raventós F, Fellin A, Ferisin G, Ferreira RJ, Ferrer A, Finy P, Gaya E, Geering ADW, Gil-Durán C, Glässnerova K, Glushakova AM, Gramaje D, Guard F, Serrudo AG, Haelewaters D, Halling RE, Hill R, Hirooka Y, Hubka V, Iliushin VA, Ivanova DD, Ivanushkina NE, Jangsantear P, Justo A, Kachalkin A, Kato S, Khamsuntorn P, Kirtsideli I, Knapp DG, Galina K, Koukol O, Kovács GM, Kruse J, Kumar TKA, Kušan I, Læssøe T, Larsson E, Lebeuf R, Levican G, Loizides M, Marinho P, Luangsa-Ard JJ, Lukina EG, Magaña V, Maggs-Kölling G, Malysheva E, Malysheva V, Martín B, Martín MP, Matočec N, McTaggart A, Mehrabi-Koushki M, Mesic A, Miller AN, Mironova P, Moreau P-A, Morte A, Müller K, Nagy LG, Nanu S, Navarro-Ródenas A, Nel W, Nguyen TH, Nóbrega T, Noordeloos ME, Olariaga I, Overton B, Ozerskaya SM, Palani P, Pancorbo F, Papp V, Pawłowska J, Thu PQ, Phosri C, Popov E, Portugal A, Pošta A, Reschke K, Reul M, Ricci GM, Rodríguez A, Romanowski J, Ruchikachorn N, Saar I, Safi A, Sakolrak B, Salzmann F, Sandoval-Denis M, Sangwichein E, Sanhueza L, Sato T, Sastoque AP, Senn-Irlet BJ, Shibata A, Siepe K, Somrithipol S, Špetík M, Pichai S, Stchigel AM, Štůsková K, Suwannasai N, Tan YP, Thangavel R, Tiago I, Tiwari S,

Tkalcec Z, Tomashevskaya MA, Tonegawa C, Tran H, Tran NT, Trovão J, Trubitsyn V, Wyk JJV, Vieira WADS, Vila J, Visagie CM, Vizzini A, Volobuev S, Vu DT, Wangsawat N, Yaguchi T, Ercole E, Ferreira BW, Souza APd, Vieira BS, Groenewald JZ (2021b) Fungal Planet description sheets: 1284–1382. Persoonia-Molecular Phylogeny and Evolution of Fungi 47: 1284–1382. https://doi.org/10.3767/persoonia.2021.47.06

Dima B, Brandrud TE, Corriol G, Jansen GM, Jordal JB, Khalid AN, Larsson E, Lorås J, Morozova OV, Naseer A, Noordeloos ME, Rossi W, Santamaria S, Sarwar S, Sesli E, Usman M, Afshan NUS, Ahmad I, Banerjee A, Banerjee K, Bendiksen E, Colombo DRdS, Kesel AD, Dovana F, Ferisin G, Hussain S, Islam S, Jesus ALd, Kaygusuz O, Krisai-Greilhuber I, Mahammad S, Mishra DK, Nath PS, Paixão SCdOd, Panja B, Papp V, Zottarelli C, Radnoti A, Rana D, Saha R, Türkekul İ, Haelewaters D (2021) Fungal systematics and evolution: FUSE 7. Sydowia 73: 271–340. https://doi.org/10.12905/0380.sydowia73-2021-0271

Fatima N, Usman M, Khalid AN (2023) *Entoloma punjabensis* sp. nov. of Rusticoides group from Chichawatni Forest, Pakistan. Phytotaxa 612(2): 217–228. https://doi.org/10.11646/phytotaxa.612.2.6

Fries E (1821) Systema mycologicum, sistens fungorum ordines, genera et species (Vol. 1). Sumtibus Ernesti Mauritti. https://doi.org/10.5962/bhl.title.5378

He XL, Li TH, Jiang ZD, Shen YH (2012) Four new species of *Entoloma* s.l. (Agaricales) from southern China. Mycological Progress 11: 915–925. https://doi.org/10.1007/s11557-012-0807-0

He XL, Li TH, Xi PG, Jiang ZD, Shen YH (2013) Phylogeny of *Entoloma* s.l. subgenus *Pouzarella* with descriptions of five new species from China. Fungal Diversity 58: 227–243. https://doi.org/10.1007/s13225-012-0212-7

He MQ, Zhao RL, Hyde KD, Begerow D, Kemler M, Yurkov A, McKenzie EHC, Raspé O, Kakishima M, Sánchez-Ramírez S, Vellinga EC, Halling R, Papp V, Zmitrovich IV, Buyck B, Ertz D, Wijayawardene NN, Cui BK, Schoutteten N, Liu XZ, Li TH, Yao YJ, Zhu XY, Liu AQ, Li GJ, Zhang MZ, Ling ZL, Cao B, Antonín V, Boekhout T, Barbosa da Silva BD, De Crop E, Decock C, Dima B, Dutta AK, Fell JW, Geml J, Ghobad-Nejhad M, Giachini AJ, Gibertoni TB, Gorjón SP, Haelewaters D, He SH, Hodkinson BP, Horak E, Hoshino T, Justo A, Lim YW, Menolli Jr N, Mešić A, Moncalvo JM, Mueller GM, Nagy LG, Nilsson RH, Noordeloos M, Nuytinck J, Orihara T, Ratchadawan C, Rajchenberg M, Silva-Filho AGS, Sulzbacher MA, Tkalčec Z, Valenzuela R, Verbeken A, Vizzini A, Wartchow F, Wei TZ, Weiß M, Zhao CL, Kirk PM (2019) Notes, outline and divergence times of Basidiomycota. Fungal Diversity 99: 105–367. https://doi.org/10.1007/s13225-019-00435-4

Izhar A, Usman M, Kiran M, Khalid AN (2022) Two new species of *Entoloma* (Entolomataceae) from Khyber Pakhtunkhwa, Pakistan. Phytotaxa 574(3): 226–240. https://doi.org/10.11646/phytotaxa.574.3.2

Karstedt F, Bergemann SE, Capelari M (2020) Five *Nolanea* spp. nov. from Brazil. Mycotaxon 135: 589–612. https://doi.org/10.5248/135.589

Katoh K, Rozewicki J, Yamada KD (2019) MAFFT online service: Multiple sequence alignment, interactive sequence choice and visualization. Briefings in Bioinformatics 20: 1160–1166. https://doi.org/10.1093/bib/bbx108

Khalid AN, Razzaq F, Naseer A, Qasim T, Kanwal S (2024) Two new species and a new record of Entolomatoid fungi (Entolomataceae, Agaricales) from Pakistan. Phytotaxa 666(1): 1–16. https://doi.org/10.11646/phytotaxa.666.1.1

Khan MB, Ishaq QM, Kiran M, Tarafder E, Fiaz M, Wen TC (2026) *Entoloma fissuromarginatum* (Entolomataceae, Agaricales), a new species from Battagram District, Pakistan. Phytotaxa 739(2): 134–144. https://doi.org/10.11646/phytotaxa.739.2.2

Kokkonen K (2015) A survey of boreal *Entoloma* with emphasis on the subgenus *Rhodopolia*. Mycological Progress 14: 116. https://doi.org/10.1007/s11557-015-1135-y

Largent DL (1994a) *Entoloma* in North America. Mad River Press, Eureka. CA (Edinburgh), 1–325.

Largent DL (1994b) Entolomatoid fungi of the Pacific Northwest and Alaska. Mad River Press, Eureka, California, USA, 495.

Matheny PB (2005) Improving phylogenetic inference of mushrooms with RPB1 and RPB2 nucleotide sequences (Inocybe; Agaricales). Molecular Phylogenetics and Evolution 35(1): 1–20. https://doi.org/10.1016/j.ympev.2004.11.014

Morgado LN, Noordeloos ME, Lamoureux Y, Geml J (2013) Multi-gene phylogenetic analyses reveal species limits, phylogeographic patterns, and evolutionary trends in the genus *Entoloma* subgenus *Entoloma*. Persoonia 31: 159–178. https://doi.org/10.3767/003158513X673521

Morozova OV, Noordeloos ME, Vila J (2014) *Entoloma* subgenus *Leptonia* in boreal-temperate Eurasia: Towards a phylogenetic species concept. Persoonia-Molecular Phylogeny and Evolution of Fungi 32: 141–169. https://doi.org/10.3767/003158514X681774

Morozova OV, Noordeloos ME, Popov ES, Alexandrova AV (2018) Three new species within the genus *Entoloma* (Basidiomycota, Agaricales) with clamped basidia and a serrulatum-type lamellae edge, and their phylogenetic position. Mycological Progress 17(3): 381–392. https://doi.org/10.1007/s11557-017-1364-3

Nguyen LT, Schmidt HA, Haeseler Av, Minh BQ (2015) IQ-TREE: A fast and effective stochastic algorithm for estimating maximum-likelihood phylogenies. Molecular Biology and Evolution 32: 268–274. https://doi.org/10.1093/molbev/msu300

Noordeloos ME (1988) *Entoloma* in North America. The species described by L.R. Hesler, A.H. Smith & S.J. Mazzer: type-species and comments. Cryptogamic Studies 2. Gustav Fischer Verlag, Stuttgart, Germany.

Noordeloos ME (1992) *Entoloma* s.l. Fungi Europaei 5. Giovanna Biella, Saronno, Italy.

Noordeloos ME (2004) *Entoloma* s.l. Fungi Europaei 5. Edizioni Candusso, Alassio, Italy, 618.

Noordeloos ME, Gates GM (2012) The Entolomataceae of Tasmania. Springer, Dordrecht, The Netherlands, 400. https://doi.org/10.1007/978-94-007-4679-4

Noordeloos ME, Lorås J, Eidissen SE, Brandrud TE, Bendiksen E, Morozova OV, Jordal JB, Weholt Ø, Jansen GM, Larsson E, Dima B (2021) Three new *Entoloma* species of the *Cyanula* clade from (sub)alpine habitats in Northern Norway and Sweden. Sydowia 73: 185–196. https://doi.org/10.12905/0380.sydowia73-2020-0185

Noordeloos ME, Dima B, Morozova OV, Reschke K, Jansen GM, Brandrud TE, Jordal JB, Bendiksen E, Vila J (2022a) *Entoloma sensu lato*. Subgenera *Cyanula*, *Leptonia*, *Nolanea*, *Trichopilus*, and the *Rhombisporum* Clade. Candusso Edtrice di Lidia Carla Candusso, Via Saronnino 41/47 I-21040–Origgio VA, Italy, 968.

Noordeloos ME, Vila J, Jordal JB, Kehlet T, Brandrud TE, Bendiksen E, Moreau P-A, Dondl M, Lorås J, Larsson E, Dima B (2022b) Contributions to the revision of the genus *Entoloma* (Basidiomycota, Agaricales) in Europe: Six new species from subgenus *Cyanula* and typification of *E. incarnatofuscescens*. Fungal Systematics and Evolution 9: 87–97. https://doi.org/10.3114/fuse.2022.09.06

Pringsulaka O, Parnmen S, Noorona N, Tacharoenmuang R, Sikaphan S, Polputpisatkula D, Uttawichai C, Naksuwankul K, Rangsiruji A (2024) Multi-locus phylogenies revealed a new record of *Entoloma* species (Basidiomycota, Agaricales) responsible for gastrointestinal poisoning. Asia-Pacific Journal of Molecular Biology and Biotechnology 32(1): 32–43. https://doi.org/10.35118/apjmbb.2024.032.1.04

Reschke K, Noordeloos ME, Manz C, Hofmann TA, Rodríguez-Cedeño J, Dima B, Piepenbring M (2022a) Fungal diversity in the tropics: *Entoloma* spp. in Panama. Mycological Progress 21: 93–145. https://doi.org/10.1007/s11557-021-01752-2

Reschke K, Morozova OV, Dima B, Cooper JA, Corriol G, Biketova AY, Piepenbring M, Noordeloos ME (2022b) Phylogeny, taxonomy, and character evolution in *Entoloma* subgenus *Nolanea*. Persoonia-Molecular Phylogeny and Evolution of Fungi 49: 136–170. https://doi.org/10.3767/persoonia.2022.49.04

Romagnesi H (1974) Essai d'une classification des rhodophylles. Bulletin Mensuel de la Société Linnéenne de Lyon 43: 325–332. https://doi.org/10.3406/linly.1974.10142

Ronquist F, Teslenko M, Mark PVD, Ayres DL, Darling A, Höhna S, Larget B, Liu L, Suchard MA, Huelsenbeck J (2012) MrBayes 3.2: Efficient Bayesian phylogenetic inference and model choice across a large model space. Systematic Biology 61: 539–542. https://doi.org/10.1093/sysbio/sys029

Vilgalys R, Hester M (1990) Rapid genetic identification and mapping of enzymatically amplified ribosomal DNA from several Cryptococcus species. Journal of Bacteriology 172(8): 4238–4246. https://doi.org/10.1128/JB.172.8.4238-4246.1990

Voglmayr H, Jaklitsch WM (2008) *Prosthecium* species with *Stegonsporium* anamorphs on *Acer*. Mycological Research 112(8): 885–905. https://doi.org/10.1016/j.mycres.2008.01.020

Werle E, Schneider C, Renner M, Völker M, Fiehn W (1994) Convenient single-step, one tube purification of PCR products for direct sequencing. Nucleic Acids Research 22(20): 4354. https://doi.org/10.1093/nar/22.20.4354

White TJ, Bruns TD, Lee SB, Taylor JW, Innis MA, Gelfand DH, Sninsky J (1990) Amplification and direct sequencing of fungal ribosomal RNA genes for phylogenetics. Academic Press, Inc, San Diego, USA, 315–322. https://doi.org/10.1016/B978-0-12-372180-8.50042-1